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Effects of light quality on growth and development, photosynthetic characteristics and content of carbohydrates in tobacco (*Nicotiana tabacum* L.) plants

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Abstract

In this study, effects of yellow (Y), purple (P), red (R), blue (B), green (G), and white (W) light on growth and development of tobacco plants were evaluated. We showed that monochromatic light reduced the growth, net photosynthetic rate (P_N), stomatal conductance, intercellular CO_2, and transpiration rate of tobacco. Such a reduction in P_N occurred probably due to the stomatal limitation contrary to plants grown under W. Photochemical quenching coefficient (q_P), maximal fluorescence of dark-adapted state, effective quantum yield of PSII photochemistry (Φ_{PSII}), and maximal quantum yield of PSII photochemistry (F_v/F_m) of plants decreased under all monochromatic illuminations. The decline in Φ_{PSII} occurred mostly due to the reduction in q_P. The increase in minimal fluorescence of dark-adapted state and the decrease in F_v/F_m indicated the damage or inactivation of the reaction center of PSII under monochromatic light. Plants under Y and G showed the maximal nonphotochemical quenching with minimum P_N compared with the W plants. Morphogenesis of plants was also affected by light quality. Under B light, plants exhibited smaller angles between stem and petiole, and the whole plants showed a compact type, while the angles increased under Y, P, R, and G and the plants were of an unconsolidated style. The total soluble sugar content increased significantly under B. The reducing sugar content increased under B but decreased significantly under R and G compared with W. In conclusion, different monochromatic light quality inhibited plants growth by reducing the activity of photosynthetic apparatus in plants. R and B light were more effective to drive photosynthesis and promote the plant growth, while Y and G light showed an suppression effect on plants growth. LEDs could be used as optimal light resources for plant cultivation in a greenhouse.

Additional key words: chlorophyll fluorescence; morphogenesis.

Introduction

Light environment, including light intensity, quality, and photoperiod, affects extensively the growth and development, and especially photosynthesis of plants (Neff *et al*. 2000, Franklin 2009). Light is not only a predominant source of energy for photosynthesis but also a signal for growth and development of plants. Many studies showed that light quality had different effects on seed germination, circadian rhythms, phototropism (Murtas *et al*. 2000, Sakai *et al*. 2001, Barrero *et al*. 2012), growth and development, phytochemicals (Li *et al*. 2009, Iacona *et al.* 2010), ultrastructure of chloroplast and anatomical structure of leaves (Liu *et al*. 2011), gene expression (Azari *et al*. 2010), disease resistance (Wang *et al*. 2010), and metabolic pathways (Sun *et al*. 2014). Recently, some

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Abbreviations: B – blue light; Car – carotenoids; Chl – chlorophyll; C_i – intercellular CO_2 concentration; DAE – days of exposure; DM – dry mass; E – transpiration rate; F_0 – minimal fluorescence of dark-adapted state; F_m – maximum fluorescence of dark-adapted state; F_v/F_m – maximum quantum yield of PSII photochemistry; FM – fresh mass; G – green light; g_s – stomatal conductance; LED – light-emitting diodes; NPQ – nonphotochemical quenching; P – purple light; P_N – net photosynthetic rate; q_P – photochemical quenching coefficient; R – red light; W – white light; Y – yellow light; Φ_{PSII} – quantum efficiency of PSII.
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researchers have investigated the effects of light quality on the plants, such as beet (Shin *et al*. 2003), grape (Heo *et al*. 2006), spinach (Matsuda *et al*. 2008), cucumber (Hogewoning *et al*. 2010), lettuce (Lin *et al*. 2013), balloon flower (Liu *et al*. 2014), *Nothofagus alpine* Oerst and *Betula pendula* Roth (Aasamaa *et al*. 2016) *etc*. However, these studies just focused on the effects of red, blue, and far-red light or their combination. These studies were usually performed under field conditions or in greenhouse. Therefore it was difficult to keep a stable experimental environment during the whole treatment, because of the weather variations during the growth season, including temperature, light intensity and duration, and humidity, which all affect greatly plant growth. Until now, it is difficult to generate precisely different light quality. The most widely used light sources are fluorescent lamps, high intensity discharge lamps, high pressure metal-halide bulbs or sodium lamps, however, these broad-spectrum lights have various limitations in application and are not consequently an optimal light source for plants growth. The use of light-emitting diodes (LEDs) has greater advantages than existing agricultural illumination; it includes high energy-conversion efficiency, wavelength specificity and narrow bandwidth, small volume, longer life, light intensity and quality adjustable and low thermal energy output so as to make it possible to irradiate close to plants as well as energy conservation (Yeh *et al.* 2009). Tobacco is an important cash crop, which is widely planted over the world. However, only the effects of red, far-red, and UV had been examined on tobacco plant earlier (Kasperbauer 1971, 1973; Andersen *et al*. 1973, Seibert *et al*. 1975). Little is known about the effects of purple, yellow, and green light on other plants. Given the above and based on our previous results (Ke *et al*. 2011, 2012; Wen *et al*. 2011, Zhao *et al*. 2012, Xu *et al*. 2013), we used LEDs to generate different monochromatic light to irradiate tobacco plants in climate chambers. The general goal of the current study was to investigate whether light quality affects growth by affecting photosynthetic apparatus and accumulation of sugars in tobacco plants after exposure to different light spectra. The aim of the study was to obtain a better understanding of the relationship between growth and photosynthesis as influenced by light quality, and to test whether LEDs could be used as an effective light source for plant cultivation.

Materials and methods

Plants and light treatment: The experiment was conducted in climate chambers at Yunnan Academy of Tobacco Agricultural Sciences Institute (24°34′N, 102°54′E) from April to August, during 2013 and 2014. Tobacco seeds (*Nicotiana tabacum* L. cv. Yunyan No87) were germinated in trays filled with a mixture of peat and vermiculite (2:1) and grown under natural light in a greenhouse. Then the seedlings were transplanted into plastic buckets (3.14 m × 0.04 m × 0.5 m) after 30 d, one seedlings per bucket, and kept growing under natural light in the field condition (average temperature of 25°C, humidity during day/night of 65/50%), till the 11th leaf expanded and the leaf length reached 2 cm; it was marked as 0 day. The plants were then transferred into the artificial climate chambers for following irradiation by different light quality. Sampling was done after 40 and 60 d (DAE) from their exposure to different light quality.

Three climate chamber rooms (*Kulan Technology Co Ltd*., Beijing, China) were used in the study. Each room contained six lamp-supporting brackets with six LEDs (*ZDL-80W*, *Nichia*, Japan), including Y, P, R, B, G, and W LEDs. The plants under W light were used as controls. All treatments were done with the same light intensity (PPFD of 350 μmol m^{-2} s^{-1}), which was monitored by quantum sensor of *LI-6400 XT* portable photosynthesis system (*LI-COR,* USA). Spectral distributions of LEDs used in this work were analyzed by *AvaSpec-2048 FT* fiber-optic spectrometer (*AVANTES*, Holland), and the characteristics of LEDs were as follows:

Color of LEDs	Wavelength [nm]	Wave crest [nm]
Yellow (Y)	570–630	585
Purple (P)	370–430	395
Red (R)	600–660	635
Blue (B)	420–480	435
Green (G)	500–560	530
White (W)	380–760	–

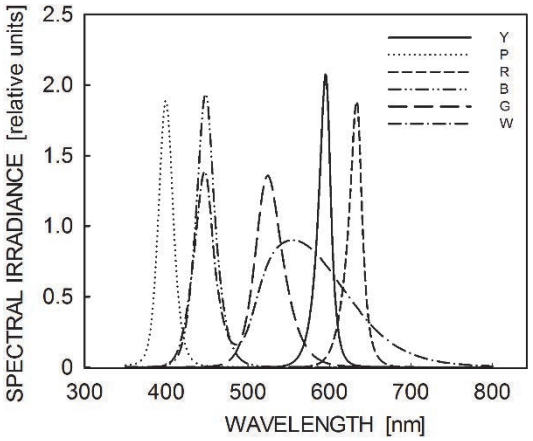

Fig. 1. Relative spectral distribution of the LEDs.

Different light-color treatments were separated by curtain in each room. In order to keep the same PPFD during a different tobacco growth stage, heights of lamp

supports were adjusted. The settings of experimental parameters, except light quality, were uniform in the climate chambers during the whole experiment. Day (07:00–20:00 h, 13 h)/night (20:00–06:00 h, 11 h), relative humidity during day/night was 65/55%, CO_2 concentration of 400 mmol^{-1}, and temperature settings were as follows:

Time [h]	Temperature [°C]	Time [h]	Temperature [°C]
00:00	14	12:00	32
01:00	12	13:00	34
02:00	10	14:00	32
03:00	12	15:00	30
04:00	14	16:00	28
05:00	16	17:00	26
06:00	20	18:00	24
07:00	22	19:00	22
08:00	24	20:00	20
09:00	26	21:00	18
10:00	28	22:00	16
11:00	30	23:00	15

Growth parameters: Plant height, length, and width of the 11th leaf were measured with a ruler on leaves attached to the plant and the ratio of length/width of leaves was calculated. Fresh samples of 11th leaves were weighed (fresh mass, FM), then exposed to 105°C and then to 80°C for drying to constant mass (dry mass, DM). Finally, the water content (%) of leaves was calculated.

Photosynthetic pigments: Chlorophyll (Chl) *a*, Chl *b*, and carotenoids (Car) were extracted by 80% cold acetone, and determined at 663 (Chl *a*), 646 (Chl *b*), and 470 nm (Car) by UV/VIS spectrophotometer (*DU800*, *Beckman*, USA) according to the method of Dere *et al.* (1998).

Photosynthetic parameters: The 11th leaf was used to analyze the P_N, stomatal conductance (g_s), intercellular CO_2 concentration (C_i), transpiration rate (E), and Chl fluorescence parameters with the *LI-6400 XT* portable photosynthesis system (*LI-COR*, USA). Measurements were performed between 9:00 to 11:00 h. The light sources of *LI-6400 XT* were used with PPDF 1,200 μmol m^{-2} s^{-1}. Minimal fluorescence (F_0), photochemical quenching coefficient (q_P), maximum fluorescence (F_m), Φ_{PSII}, F_v/F_m, and nonphotochemical quenching (NPQ) were measured by *LI-COR* and caculated according to van Kooten *et al*. (1990) and Maxwell *et al*. (2000).

Total soluble sugars and reducing sugar contents: Dry leaf samples (0.1 g, DM) were immersed into 2 ml of 80% ethanol, extracted in water bath at 80°C, and then centrifuged three times (10,000 × *g*, 20 min). The combined liquid supernatants were destained by activated carbon and constant volume was adjusted in 100-ml volumetric flask. Total soluble sugar and reducing sugar contents were measured by the colorimetry of sulfuric acid-anthrone and 3, 5-dinitrosalicylic acid methods unsing UV/VIS spectrophotometer (*DU800*, *Beckman*, USA) at 630 and 540 nm, respectively (Buysse *et al.*1993).

Statistical analysis: In this study, 24 plants (replications) were used in each treatment. All statistical analyses were conducted using *SPSS 11.5* (NY, USA) with the *Tukey*'s text (P<0.05), and the means and standard error (SE) were performed by analysis of variance (*ANOVA*) procedure using multiple comparisons. The figures were drawn with *Sigmaplot 10.0* (*Systa software Inc*., Chicago, IL, USA).

Results

Growth and morphological characteristics: Plant height, length, and width of leaves gradually increased under different monochromic lights from 40 to 60 DAE (Fig. 2). Under W, the plants were the tallest (61.7 cm), followed by these under R, P, B, Y, and G; all plants were significantly smaller by 14, 17, 19, 30, and 39%, respectively, as compared with W at 40 DAE. The same results were observed at 60 DAE (Fig. 2*A*). Under R, the plants exhibited the longest leaf (62.3 cm), which was a significant enhancement by 16%, while it was significantly reduced under Y, G, and B by 21, 22, and 25%, respectively, compared with these under W (54.6 cm) at 40 DAE. The same phenomenon was also observed at 60 DAE (Fig. 2*B*). Under W, plants possessed the maximum leaf width (23.0 cm), followed by these under P, B, G , and Y and a significant reduction by 15, 31, 36, and 44%, respectively, compared with these under W at 40 DAE. It was also observed at 60 DAE (Fig. 2*C*). Under Y, plants showed the highest ratio of length/width of leaves (3.31), followed by G (2.93), R (2.82), and P (2.81), which all significantly increased by 40, 24, 20, and 19%, respectively, compared with these under W (2.36) at 40 DAE. The tendency of 60 DAE was the same (Fig. 2*D*).

Photosynthetic pigments and water content: Chl *a,* Chl *b*, and Car contents gradually declined under different monochromic lights from 40 to 60 DAE (Fig. 3). At 40 DAE, the plants grown under R showed the maximum contents of Chl *a* [2.62 mg g^{-1}(FM)], which was significantly 40% higher than those under W, while it significantly decreased under Y, P, and B, which represented a significant decline by 4, 32, and 35% compared with W, respectively (Fig. 3*A*). Under R, the plants showed the maximum content of Chl *b* [1.16 mg g^{-1}(FM)] and a significant increase by 5%, while it decreased under G, Y, P, and B, which represented significant reductions by 5, 10, 40, and 43%, respectively, compared with W after 40 DAE (Fig. 3*B*). Total Chl contents reached the

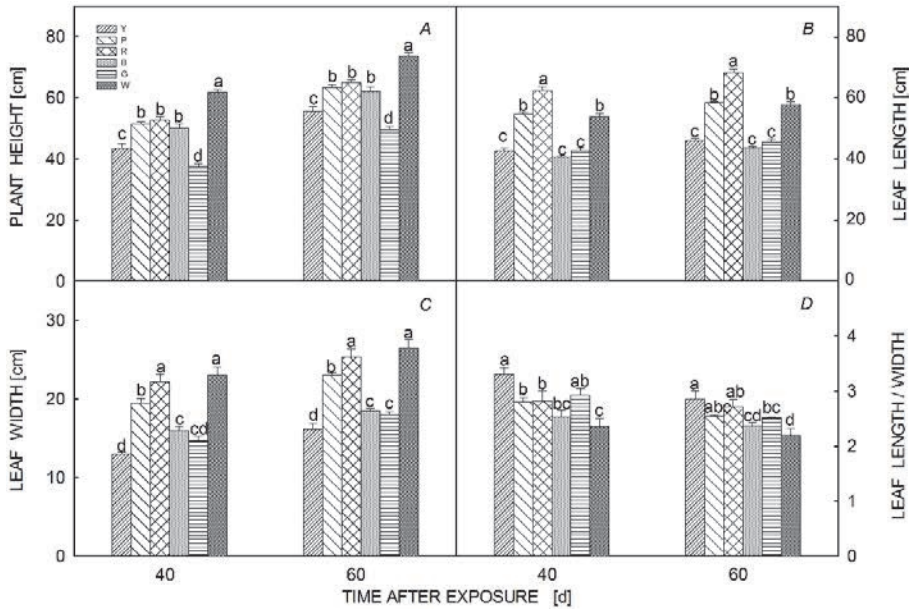

Fig. 2. Effects of different light quality on plant height (*A*), length (*B*), width (*C*) and ratio of leaves length/width (*D*) of tobacco after 30 and 60 DAE. Yellow (Y), purple (P), red (R), blue (B), green (G), and white (W) light. Significant differences are marked by *different letters*.

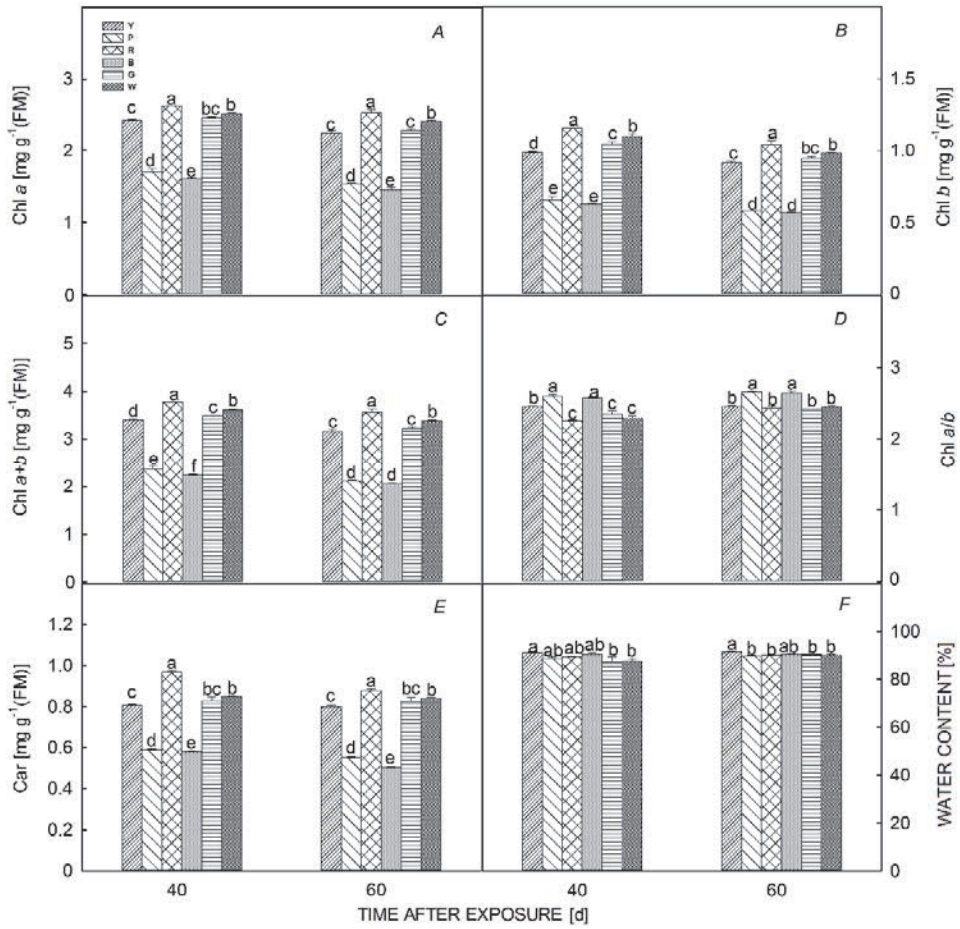

Fig. 3. Effects of different light quality on content of chlorophyll *a* (*A*), chlorophyll *b* (*B*), chlorophyll *a+b* (*C*), chlorophyll *a/b* (*D*), carotenoid (*E*) and water content (*F*) of tobacco leaves after 30 and 60 DAE. Yellow (Y), purple (P), red (R), blue (B), green (G), and white (W) light. Significant differences are marked by *different letters*.

maximum under R [3.78 mg g^{-1}(FM)], significantly increased by 5%, but was reduced under G, Y, P, and B, which presented significant reductions by 3, 6, 34, and 38%, respectively, compared with W [3.61 mg g^{-1}(FM)] at 40 DAE (Fig. 3*C*). At 40 DAE, the plants under R showed the maximum content of Car, which was 0.97 mg g^{-1}(FM) and 14% significantly higher than that of W, but lower under Y, P, and B, which was a significant lowering by 5, 31, and 32% compared with those under W (Fig. 3*E*). In addition, the plants under P and B showed minimum Chl *a*, *b*, total Chl as well as Car compared with W, in contrast to the plants under Y, P, and B showing a higher ratio of Chl *a*/*b*, which were 2.46, 2.57, and 2.6 and 7, 12, and 14% higher than that of W (2.29) at 40 DAE (Fig. 3*D*). The tendency of the Chl *a*, Chl *b*, and Car contents at 60 DAE corresponded to those at 40 DAE. Under Y, the plants showed the maximum water content (91.4%), significantly increased by 3%, compared with W (89.1%) at 40 DAE. The same result was also observed at 60 DAE (Fig. 3*F*).

Photosynthetic characteristics: P_N, g_s, C_i, and E of plants gradually decreased under different monochromic lights from 40 to 60 DAE (Fig. 4). Under W, the plants showed the greatest P_N [6.52 μmol(CO_2) m^{-2} s^{-1}], followed by these under P, B, R, G, and Y [1.33 μmol(CO_2) m^{-2} s^{-1}], which all were significantly reduced by 30, 57, 65, 77, and 83%, respectively, as compared with W at 40 DAE. Under W, the plants showed maximum P_N [2.62 μmol(CO_2) m^{-2} s^{-1}],but it significantly decreased under P, B, R, G, Y [0.52 μmol(CO_2) m^{-2} s^{-1}], which all showed reduction by 32, 36, 54, 60, and 79%, respectively, compared with those under W at 60 DAE (Fig. 4*A*). The variation trends of g_s, C_i, and E corresponded with P_N (Fig. 4*B–D*).

Chl fluorescence parameters: F_0, q_P, Φ_{PSII}, and NPQ of plants gradually decreased under different monochromic lights from 40 to 60 DAE (Fig. 5*A,B,D,F*). Under P, the plants showed the greatest F_0, followed by these under B, R, G, Y, and W, which all significantly increased by 19, 13, 9, and 4%, respectively, as compared with W at 40 DAE (Fig. 5*A*). Under W, the plants showed the greatest q_P (0.79), followed by these under P (0.75), B (0.74), R (0.71), G (0.67), and Y (0.59), which all significantly decreased by 5, 6, 10, 15, and 25%, respectively, as compared with W at 40 DAE (Fig. 5*B*). The tendency of Φ_{PSII} corresponded with q_P (Fig. 5*D*). Under W, the plants showed the highest F_m, followed by P, B, R, G, and Y, which all were reduced by 2, 2, 2, 2, and 4%, respectively, as compared with W at 40 DAE (Fig. 5*C*). The variation of the F_v/F_m ratio was consistent with the F_m (Fig. 5*E*). Plants under Y showed the maximum NPQ (1.07), followed by G (0.54), R (0.18), B (0.15), with the lowest values under W (0.1), which represented a significant increase by 970%, 440%, 80% and 50%, respectively, as compared with W at 40 DAE (Fig. 5*F*). The same trend was also observed at 60 DAE (Fig. 5).

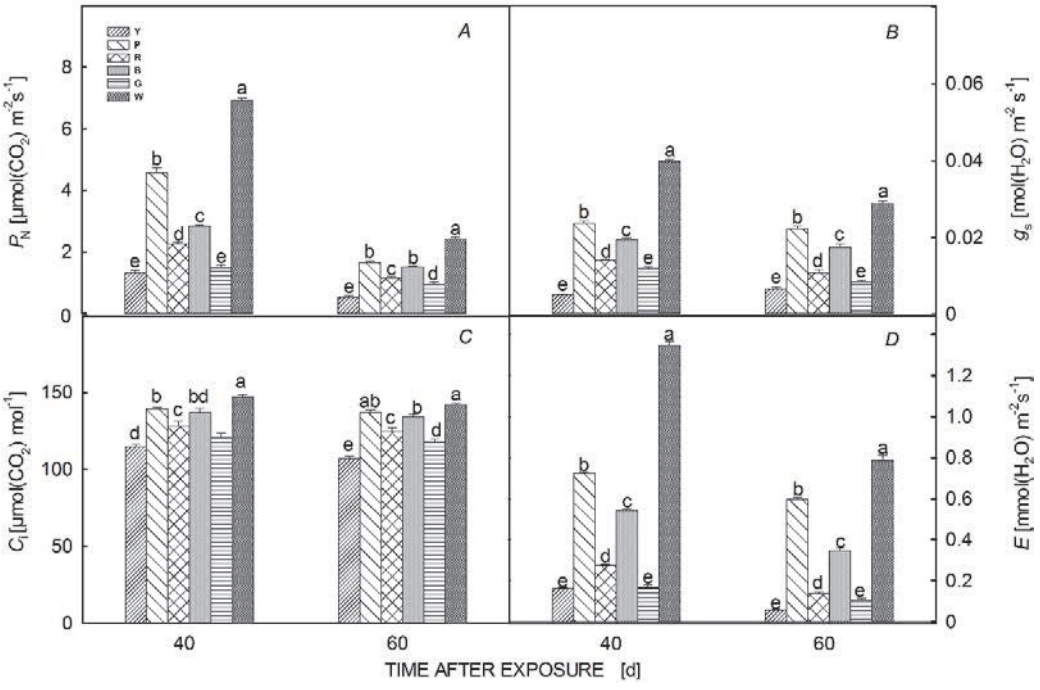

Fig. 4. Effects of different light quality on the photosynthesis of tobacco leaves. (*A*) net photosynthetic rate (P_N); (*B*) stomatal conductance (g_s); (*C*) intercellular CO_2 contentration (C_i); (*D*) transpiration rate (E) after 30 and 60 DAE. Yellow (Y), purple (P), red (R), blue (B), green (G), and white (W) light. Significant differences are marked by *different letters*.

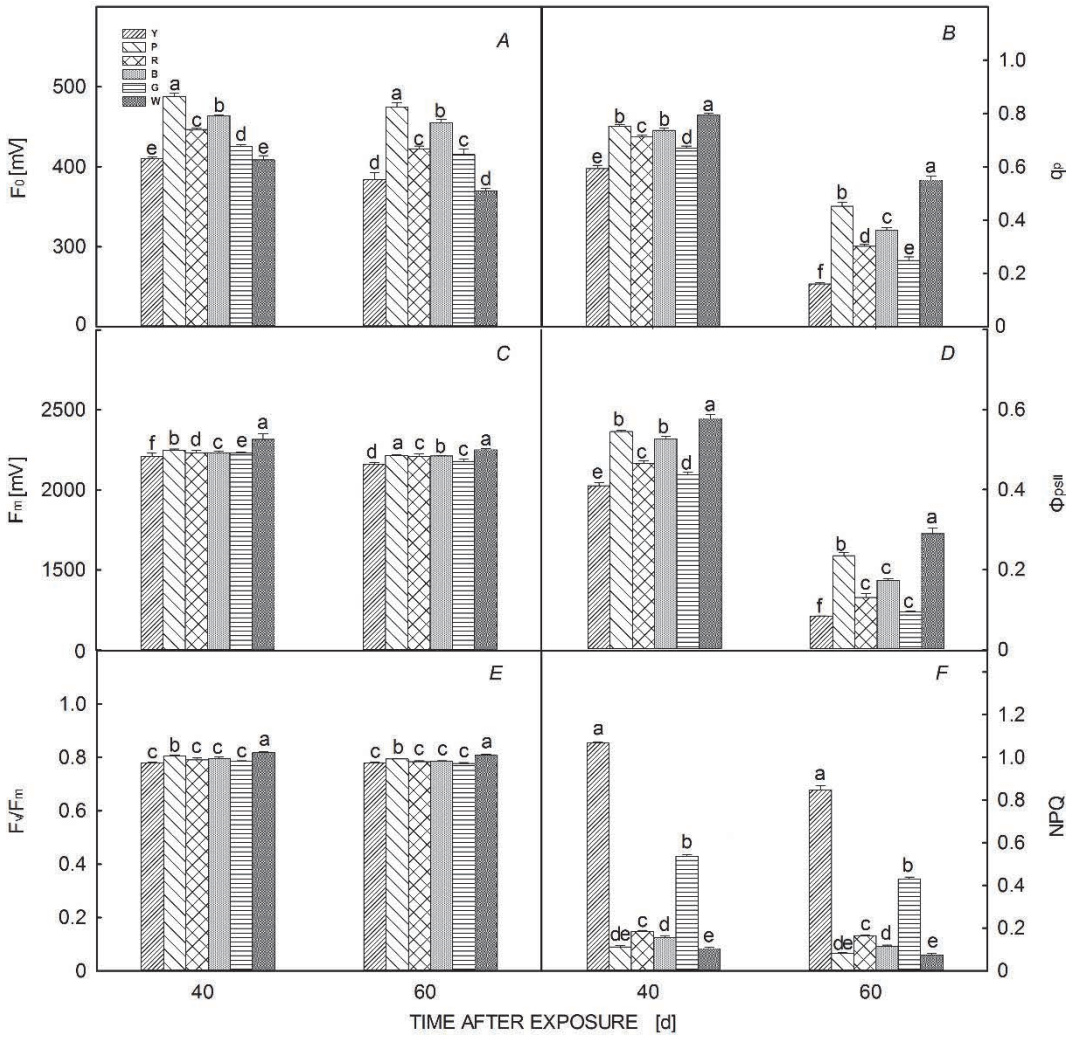

Fig. 5. Effects of different light quality on the chlorophyll fluorescence of tobacco leaves after 30 and 60 DAE. (*A*) minimal fluorescence of the dark-adapted state (F_0); (*B*) photochemical quenching coefficient (q_P); (*C*) maximal fluorescence of the dark-adapted state (F_m); (*D*) effective quantum yield of of PSII photochemistry (Φ_{PSII}) (*E*) maximum quantum yield of PSII photochemistryl (F_v/F_m); (*F*) nonphotochemical quenching (NPQ). Yellow (Y), purple (P), red (R), blue (B), green (G), and white (W) light. Significant differences are marked by *different letters*.

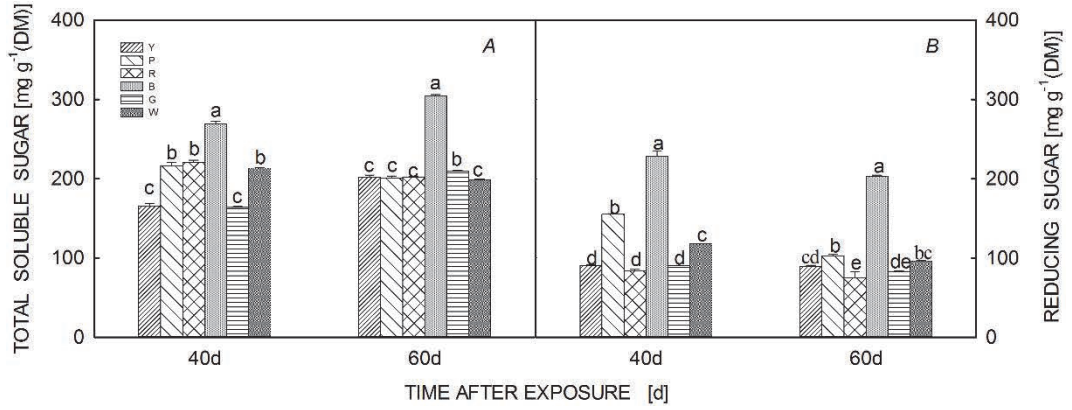

Fig. 6. Effects of different light quality on the contents of total soluble sugar (*A*) and reducing sugar (*B*) of tobacco leaves after 30 and 60 DAE. Yellow (Y), purple (P), red (R), blue (B), green (G), and white (W) light. Significant differences are marked by *different letters*.

Total soluble sugar and reducing sugar contents: Plants grown under B showed the maximum contents of total soluble sugar, which was 268.7 mg g^{-1}(DM) and 26% higher than those grown under W [212.71 mg g^{-1}(DM)]. A significant decline was observed under Y and G, which was 22 and 23% lower than in those grown under W, respectively at 40 DAE. At 60 DAE, the plants grown under B showed the maximum contents of total soluble sugar, followed by G, which were 26 and 5% higher than that of W [195.65 mg g^{-1}(DM)], respectively (Fig. 6*A*).

Under B and P, the plants showed the greatest content of reducing sugar, 228.34 and 155.28 mg g^{-1}(DM), which significantly increased by 93 and 32%, as compared with W. The Y, G, and R plants showed 23, 24, and 29% lower contents compared with W, respectively, at 40 DAE. At 60 DAE, under B, the plants showed the greatest content of reducing sugar, which was 202.92 mg g^{-1}(DM) representing a significant increase by 112%, as compared with W [95.89 mg g^{-1}(DM)] followed by Y, G, and R with their 6, 13, and 22% lower contents compared with W, respectively (Fig. 6*B*).

Discussion

In this study, plant growth, photomorphogenesis, photosynthesis, and sugar contents were significantly influenced by light quality. Plants use several pigments to sense the light spectrum under different irradiance conditions as light components are varying from twilight to sunset. A phytochrome receptor is the receptor of red/far red light, while ultraviolet and blue light is absorbed by crytochrome and phototropins (Folta and Childers 2008). Our results proved that plants grown under monochromatic lights, as compared with those under white light, showed a reduction of their plant height (Fig. 2*A*). Previous results demonstrated that red light accelerated the elongation of the stem in some plant species, such as chrysanthemum, pepper, and *Phalaenopsis* (Schuerger *et al*. 1997, Kim *et al*. 2004, Shin *et al*. 2008). Here, we also observed that R light promoted the growth of stem in tobacco plants, but less than those under W light. These differences could be attributed to the R light showing different effects on the elongation of the stem at different stages of plant growth. It can lead to an imbalance of light energy distribution between PSII and PSI, and the growth of plants is inhibited (Tennessen *et al*. 1994). The plants grown under Y and G showed the lowest plant height, which agreed with the report of Su *et al*. (2014) suggesting that Y and G light show an inhibiting effect on the growth of plants.

In this study, we observed that the length and width of tobacco leaves under Y, G, and B light decreased significantly, except that under R light, where the plants showed the longest leaves compared with those under W light. Our results showed that R light promoted the elongation and extension of tobacco leaves. This phenomenon could be attributed to the higher phytochrome content under red light which promoted the cell division and expansion of plants (Neff *et al*. 2000), while the blue light showed an inhibting effect. The same results had also been observered in lettuce, wheat, and *Doritaenopsis* (Goins *et al*. 1997, Shin *et al*. 2008, Li *et al*. 2009). However, the ratio of the leaf length/width was higher under Y, P, R, and G light compared with this under W light and the tobacco leaves were longer and narrower, which is consistent with our previous research (Ke *et al*. 2011). It means that different lights showed an inhibiting effect on the growth of tobacco plants compared with white light, the same results were also observed in pepper, lettuce, spinach, and radish (Brown *et al*. 1995, Neil *et al*. 2001, Kim 2004).

Meanwhile, the growth of leaves under different monochromatic light showed a bigger angle between the stem and petiole and declination in order to obtain more irradiation, compared with those under W light. This phenomenon has also been observed in other plants and classified as a shade avoidance (Franklin *et al*. 2008). On the contrary, tobacco leaves under B light showed the smaller angle between the stem and petiole, which might be attributed to the function of phototropin, a kind of blue light receptor, and showing a phototropism (Briggs *et al*. 2002). In addition, the plants under B light showed a compact plant types, compared with those under white light. Such a result has been also observed when the plant species, such as radish, pea, and wheat, were growing under higher intensity of blue light (Cope *et al*. 2013). It indicates that the photomorphogenesis of tobacco plants was influenced by monochromic light, and blue light plays an important role in leaf morphological development.

In our study, we observed that plants under R light showed the higher content of Chl *a*, Chl *b*, total Chl, and Car, but it significantly decreased under Y, P, and B light compared with those under W light (Fig. 3). This result indicated that R light showed a promoting effect on the accumulation of Chl and Car. However, it is not consistent with the results on pea, grape, and cotton, where Chl contents of plants increased under blue light but decreased under red light (Wu *et al*. 2007, Poudel *et al*. 2008, Li *et al*. 2010). The difference could be caused by different plants and experimental environments used. Under B and P light, plants showed a lower content of Chl *a*, Chl *b*, total Chl, and Car, but a higher ratio of Chl *a*/*b* compared with those under W light. The same result was also found in cucumber and lettuce (Wang *et al*. 2009, Johkan *et al*. 2010). Changes in Chl *a*/*b* were considered an indicator for relative photosystem stoichometry and reflected the changes in the size of the PSII light-harvesting antenna and PSII:PSI content (Leong *et al*. 1984, Pfannschmidt *et al*. 1999). This interpretation is also supported the Chl fluorescence results in our experiment, where the lower Φ_{PSII} was under Y, R, and G light. Compared with the

plants under W light, Y light increased the water content of leaves significantly.

Plants grown under different monochromatic lights, compared with W, showed a lower P_N which exactly corresponded to the g_s, C_i, and E (Fig. 4). Therefore, we could suggest that the reduction in P_N under different light quality occurred perhaps due to the stomatal limitation, compared with the plants under W. It was also observed in chrysanthemum (MacMahon *et al*. 1991), wheat (Goins *et al*. 1997), pepper (Schuerger *et al*. 1997), acacia (Yu and Ong 2003), and cucumber (Wang *et al*. 2009). In our study, plants under P, R, and B light showed the higher P_N. It exactly correlated with the absorption spectra of photosynthetic pigments; Chl and Car have high light absorption at 400–500 nm and at 630–680 nm, respectively, and low light absorption at 530–610 nm (Pfündel 1990). However, plants grown under red light did not show the highest P_N as compared with other studies. This could be attributed to the shift of the wavelength (the maximum intensity was at 635 nm) applied in our study; as reported earlier, the highest photosynthetic activity was found within the red range of 655–660 nm (Fankhauser *et al*. 1997). Moreover, plants grown under Y and G showed the lowest P_N, which is cosistent with earlier study reporting that yellow and green light limited growth and development of plants (Dougher *et al*. 2001, Folta *et al*. 2007). The lower P_N under green and yellow light could be caused by lower Rubisco protein content, lower Rubisco carboxylase and lower *rbc*, *rca* expression, contrary to increased P_N under purple, red, and blue light (Ke *et al*. 2012, Su *et al*. 2014). Therefor, the different P_N of plants under different light quality was observed under the same light intensity in our study. When plants, such as chrysanthemum, *Withania somnifera* (L.) Dunal, and lettuce were grown under red or other monochromatic light combined with the blue light, plants showed higher P_N as compared to those under monochromatic light (Kim *et al*. 2004a, Lee *et al*. 2007, Lin *et al*. 2013). It indicated that plants under multi-wavelength irradiation showed an higher photosynthetic characteristics than those under monochromatic lights. In this study, the decrease in P_N from 40 DAE to 60 DAE under different monochromatic lights could be attributed to the stomatal limitation factors and to the decrease in Chl and Car contents or due to the decreasing activity of photosynthetic apparatus during the process of senescence in tobacco leaves. Our results suggested that different monochromatic lights showed an inhibiting effect on the photosynthesis of plants compared with those plants grown under a broad spectrum of white light.

Plants can acclimated to the different light environment by regulating the proportion of PSI and PSII as well as the size of the antenna pigments (Jensen *et al*. 2007). It has been known that changes in Chl fluorescence emission from photosynthetic organisms are frequently indications of changes in their photoynthetic activity (Baker *et al*. 2004). Overall, different monochromatic light decreased the q_P, F_m, Φ_{PSII}, and F_v/F_m, whereas inreased F_0 and NPQ of tobacco leaves compared with W, which corresponded to the variation of P_N in tobacco plants under different light quality (Fig. 5).

Previous study showed that a lower F_0 always accompanies lower Chl contents and it increases when the reaction center is damaged under stress conditions (Schnettger *et al*. 1994). In this study, we found that different monochromatic lights, except yellow light, increased the F_0 in tobacco plants. It suggested that different monocharomatic lights damaged or inactivated the reaction center of PSII (Demmig-Adams *et al.* 1989) in comparison with white light; it correlated with the changes of P_N. However, in our study, we did not find a significant relationship between the total Chl contents and F_0. Plants grown under different monochromatic lights showed lower F_m than those in W at 60 DAE. It indicated that plants grown under W showed Q_A in reduced state to a greater extent than those grown under Y, P, R, B, and G.

When plants grew under a favourable environment, F_v/F_m is kept in a stable range but it decreases, when plants grow under the adverse environment (Allen *et al*. 2001). A lower F_v/F_m than that of the W plants was observed under different monochromatic lights, which could be attributed to the inactivation of the reaction center of PSII resulting in the photoinhibition (Krause *et al*. 1991).

In this study, plants under different monochromatic lights reduced their q_P significantly compared with W, which indicated that plants grown under white light showed a higher degree of opening of reaction center, oxidative level of primary quinone acceptor, and energy harvesting effciency of PSII than those plants under Y, P, R, B, and G (Lefebvre *et al*. 2005, Miyake *et al*. 2009). However, the plants under G and Y showed the maximum degree of closed reaction centers of PSII and showed a maximum inhibiting effects on photosynthesis.

Higher Φ_{PSII} unually indicated higher photosynthetic efficiency and high efficiency of electron transfer (Miyake *et al*. 2009). In our study, Φ_{PSII} of plants under different monochromatic lights was lower than those under W. It was consistent with the variation of q_P. The results indicated that plants under W kept a higher photon absorbing rate, efficiency of electron transfer rate, and $NADP^+$ and ADP regeneration capacity of PSII than those plants under different monochromatic lights and the decline of Φ_{PSII} occurred mostly due to the reduction in q_P.

In this study, we found that the plants grown under Y and G showed significantly higher NPQ than those under W. It indicated that plants grown under Y and G lost more energy in the form of thermal dissipation from the reaction center of PSII and showed the lower photosynthetic capacity, which is a protective mechanism of photosynthetic apparatus (Badger *et al*, 2000). While the plants grown under B and P kept a higher P_N in order to avoid the damage of the photosynthetic apparatus, because of the higher energy of B and P light.

We concluded that the reduction of Φ_{PSII} and F_v/F_m and the increase in F_0 indicated the damage or inactivation of

the reaction center of PSII under different monochromatic lights. Therefore, we suggested that different light quality inhibited the photosynthesis of plants and reduced the activity of photosynthetic apparatus.

Carbohydrates are not only one of products of photosynthesis but also take part in the regulation of the photosynthesis, growth, and development of leaves with the feedback mechanism (Paul *et al*. 2003). Total soluble sugar contents of plants grown under Y and G were reduced significantly but increased under B compared with W. The reducing sugar content of plants grown under P and B increased significantly but declined significantly under Y, R, and G at 40 DAE. Overall, plants grown under B showed the higher contents of total soluble sugars and reducing sugars (Fig. 6), and this results was different from that of Li *et al* (2010), which showed that the total soluble sugar content of upland cotton grown under red light was the highest one. However, it was in agreement with results of Wang *et al.* (2009) and Heo *et al.* (2006), who showed that the total soluble sugar content of *Cucumis sativus* seedling and the reducing sugar content of grape grown under blue light were the highest ones. Thus, we suggested that blue light exhibited a promoting effect on the biosynthesis and accumulation of soluble and reducing sugars. This could be caused by higher activity of Calvin cycle enzymes under blue light. Ke *et al.* (2012) and Wang (2009) have also observed that under blue light plants showed higher Rubisco carboxylase activity and related gene expression of Calvin cycle enzymes.

In conclusion, different monochromatic lights caused limited growth and development of plants, compared with white light, which correlated with the reductions in growth, photosynthetic, and Chl fluorescence parameters. Among different monochromatic lights, red and blue light were more effective to drive photosynthesis and promote the plant growth, while yellow and green light were less effective and showed an suppression effect on plant growth. Blue light promoted the biosynthesis and accumulation of total soluble sugar and reducing sugar, while the reducing sugar contents declined under red and green light. Thus, a proper combination of blue and red light might provide more suitable light environment for plant cultivation in greenhouse. LEDs could be widely used as light sources for plant cultivation. Precise climate chamber could provide an optimal environment for plant research.

In order to understand well how light quality affects the growth, photosynthesis, and carbohydrate contents, it would be necessary to examine the activity of key enzymes in photosynthesis and carbohydrates metabolism, such as Rubisco, sucrose phosphorylase *etc*., and their gene expression. More physiological parameters and the combination of different monochromatic lights should be considered and analyzed in order to interpret the biological function and action mechanisms.

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